Thaiszia - J. Bot., Košice, 32 (1): 029-054, 2022
https://doi.org/10.33542/TJB2022-1-03

THAISZIA
JOURNAL OF BOTANY

The genus *Woodsia* R. Br. in Ukraine (Woodsiaceae)

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Bezsmertna O., Hleb R., Orlov O., Vasheniak I., Podpriatov O., Kvakovska I., Danylyk I., Kamleitner K., Ragulina M., Babytskiy A., Rubanovska N. & Lysenko T. (2022): The genus *Woodsia* R. Br. in Ukraine (Woodsiaceae). – Thaiszia – J. Bot. 32 (1): 029-054.

Abstract: Two species of the genus *Woodsia* R. Br. have been reported for Ukraine: *W. alpina* (Bolton) Gray and *W. ilvensis* (L.) R. Br. Based on our

analysis of the literature data and the herbarium specimens of 53 herbaria from Ukraine, Austria, Czech Republic, Hungary, Poland, Russia, Romania and Slovak Republic, we present maps of the distribution of the genus in Ukraine showing correct, unconfirmed and erroneous records. Our results show a changed perception of the distribution pattern of *Woodsia* genus, particularly the distribution of *W. alpina*. The records of *W. alpina* in the Ukrainian Carpathians were erroneous, only *W. ilvensis* is growing here, and *W. alpina* in Ukraine has been convincingly confirmed only from Donetsk, Luhansk and Zaporizhzhya region (Steppe zone of Ukraine), from very low elevation making these sites the lowest in continental Europe. In addition to the distribution analysis, we have focused on a morphological overview of *Woodsia* species and their ecological affinities in Ukraine. A re-evaluation of the threat status of *Woodsia* species, using IUCN criteria, concludes that both species should be assessed as Critically Endangered (CR) in Ukraine.

Keywords: *Woodsia*, rare species, morphology, distribution, population, phytosociology.

Introduction

Genus *Woodsia* R. Br. includes about 25 species distributed all over the world, except Australia and Antarctica. The most likely place of origin of the genus is Central Asia (Gladkova 1978). Two species of this genus are known in the territory of Ukraine, mentioned since the beginning of the 19th century. Some of the earliest records of the genus are found in the publication of Ledebour (1853). In the 20th century some information concerning these species was given by Gajewski (1937), Fomin (1926, 1938) and others. *Woodsia alpina* (Bolton) Gray was repeatedly reported from the Kam'yani Mohyly Nature Reserve (Donetsk region) (specimen deposited in DNZ, KW, LWKS and other herbaria), while *W. ilvensis* (L.) R. Br. was frequently collected from the vicinity of Zhytomyr city (Zhytomyr region) (vouchers deposited in KW, LE, LW and other herbaria). However, there have also been some rather surprising and doubtful records reported in the literature, including references to *W. alpina* from the territory of Zakarpattia, Ivano-Frankivsk, Zaporizhzhya, Luhansk and Donetsk regions of Ukraine (Popovych et al. 1992; Didukh et al. 2000; Didukh 2009; Shelegheda & Shelegheda 2017). *Woodsia ilvensis* has been reported from Zakarpattia, Zhytomyr and Zaporizhzhya regions (Popovych et al. 1992; Didukh et al. 2000; Didukh 2009), as well as from the Autonomous Republic of Crimea (Pallas 1975; Wulf 1923). Such improbable and ambiguous records prompted the current study to research and revise the locations of *Woodsia* in Ukraine, assess the state of populations of the genus, and analyse the ecological features of both species.

Material and Methods

Revision of locations

We examined herbarium specimens of *Woodsia* deposited in 53 scientific institutions in Ukraine, Austria, Czech Republic, Hungary, Poland, Russia, Romania

and Slovak Republic (acronyms follow Thiers (2016+)): BP, BRA, BRNU, BUC, CHER, CL, CWU, DNZ, DSU, GJO, GZU, I, IAGB, IASI, KHER, KO, KRA, KRAM, KW, KWHU, KWHA, LE, LWS, LWKS, LW, MELIT, MSUD, PR, PRC, PWU, SAV, SLO, SOF, UU, W, WA, WABG, WRSL, WU, YALT. Additional material was examined from other regional herbaria (acronyms non officially confirmed in the international database): Iasi Museum of Natural History (Romania), Taras Shevchenko National University of Kyiv (Ukraine), Lviv National Forestry Engineering University (Ukraine), Lesya Ukrainka Volyn National University (Ukraine), Volyn Museum of Local Lore (Ukraine), Rivne National University of Water and Nature Management (Ukraine), Rivne Natural History Museum (Ukraine), Volodymyr Hnatyuk Ternopil National Pedagogical University (Ukraine), Kryvyi Rih Botanical Garden (Ukraine), T. H. Shevchenko Chernihiv State Pedagogical University (Ukraine), Kamianets-Podilsky Ivan Ohienko University (Ukraine), Vasyl Stefanyk Prykarpatskyi University (Ukraine), Ferenz Rakoczy II Transcarpathian Institute (Ukraine). Some specimens from herbaria collections were evaluated with the assistance of colleagues from many scientific institutions (Austria, Czech Republic, Hungary, Romania, Slovak Republic). Electronic resources, such as the virtual herbarium management system JACQ, have also been investigated (https://herbarium.univie.ac.at/database/collections.htm).

The locations of the studied species are indicated in accordance with the present administrative divisions of Ukraine and recent topology. Based on the results of our analysis of the literature data and herbarium specimens of the above-mentioned institutions, we made maps of *Woodsia* species distributions in Ukraine showing confirmed and erroneous records. Maps and charts have been made with the help of Quantum GIS 3.16.5 Hannover (https://www.qgis.org/uk/site/).

Species determination

Determination of the species are generally based on the morphological features, keys and protologs by Linnaeus Carl (1753), Bolton James (1790), Brown Addison Nathaniel Lord Britton (1810), Gray Samuel Frederick (1821), Butters (1941), Vasheka & Bezsmertna (2012), Jäger et al. (2017).

Phytosociological characteristics: data sampling and species nomenclature

Numerous expeditionary trips, as well as gathering and processing of the literature sources were conducted during 2008–2021. Six relevés with plot sizes ranging from 0.5 to 10 m^2 using the Braun-Blanquet (1936) approach were prepared. Data was stored in both TURBOVEG (Hennekens & Schaminée 2009) and the Ukrainian Grassland Database (EU-UA-001; Kuzemko 2012). The nomenclature of taxa follows Euro+Med PlantBase (2006). Higher syntaxonomic units are given according to Mucina et al. (2016) and Bardat & Hauguel (2002). Bryophyte nomenclature follows Hodgetts et al. (2020) and Boiko (2008, 2014) and lichens follow the international database of *Index Fungorum* (http://www.indexfungorum.org/Names/Names.asp) and Kondratiuk (1998).

Conservation and species threat status

Categories of threat status are listed according to IUCN (2012). The red list threat status in the territory of Ukraine and adjacent territories (Poland, Hungary, Slovak Republic, Czech Republic and Romania), where the studied species are present, was assessed by different literature sources (Király 2007; Didukh 2009; Dihoru & Negrean 2009; Turis et al. 2014; Eliáš et al. 2015; Kaźmierczakowa et al. 2016; Grulich & Chobot 2017).

Results and Discussion

Morphology of *Woodsia* species

Only two species of the *Woodsia* genus are reported from Ukraine (Mosyakin & Fedoronchuk 1999; Didukh 2009) – *W. alpina* and *W. ilvensis* (Fig. 1, 2).

For precise and better identification of these species in the field, here we present their comparative morphological description (highlighted features of the species). Both species of the *Woodsia* genus are small plants with height varying from 5 to 25 cm, with a short, multi-pinnate rhizome covered with scales. Their fronds are monomorphic and summer-green, growing in a rosette. The petiole is shorter than the leaf blade and has an articulation near the middle (*W. ilvensis*) or at the base (*W. alpina*). Throughout its full length (including the rhachis), the petiole is also covered with ramenta. The most noticeable differences have been observed in the leaf blade. In *W. alpina*, the leaf blade is narrowly lanceolate, bipinnately-divided; in the adult state it is almost fully glabrous or covered with scattered fuzz. In *W. ilvenis*, the leaf blade is lanceolate, bipinnately-divided, dark green and covered with light brown fuzz on both sides, while its scales are located only on the abaxial side along the median veins. The primary segments of *W. alpina* are sessile, distinctly narrowed at the base, ovate or broadly ovate, pinnately-divided or pinnately-lobed, as well as rounded at the apex. In *W. ilvensis*, the primary segments are sessile, distinctly

Fig. 1 *Woodsia alpina* in the Kam'yani Mohyly Nature Reserve (Ukrainian Steppe Natural Reserve of the National Academy of Sciences of Ukraine). Photo by Olesya Bezsmertna.

Fig. 2 *Woodsia ilvensis* in the Mount Kobyla (near the village of Kobyletska Poliana, Zakarpattia region). Photo by Olesya Bezsmertna.

narrow at the base, lanceolate or elongated ovate, pinnately-divided, as well as rounded at the apex (Fig. 3).

We consider *W. alpina* and *W. ilvensis* to be clonal herbs which possess organs of clonal growth, enabling them to make fragments during their life cycle and to form independent units (rosettes, ramets or clones) by vegetative reproduction; the whole plant reproduces sexually several times during its lifespan, while individual ramets (rosettes or clones) may reproduce once or several times during their lifespan (Vasheka & Bezsmertna 2012).

Some Ukrainian sources noted that natural hybrids between these two species occur (Mosyakin & Fedoronchuk 1999; Chopyk & Fedoronchuk 2015). In particular, the hybrid *W*. ×*gracilis* (Lawson) Butters has been described from southeastern Canada (Tsvelev 2005a, b). Morphologically *W*. ×*gracilis* is more similar to *W. alpina*, but has some ramenta on the petiole, rachis and lower surface of the fronds. Its sori remain undeveloped for its entire life. However, in our opinion, this hybrid can be confused with young plants of *W. ilvensis* that may also have underdeveloped sori (Lawson 1864; Tsvelev l. c.). Although *W*. ×*gracilis* has been reported from Ukraine (Mosyakin & Fedoronchuk 1999; Chopyk & Fedoronchuk 2015), we have only considered the distribution and ecology of the two species *W. alpina* and *W*. *ilvensis*.

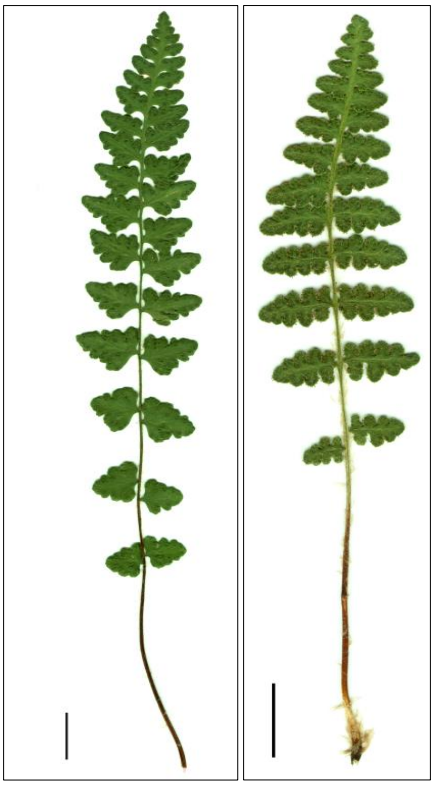

Fig. 3 General view of the fronds of *Woodsia alpina* (A; Kam'yani Mohyly Nature Reserve, Ukrainian Steppe Natural Reserve of the National Academy of Sciences of Ukraine) and *W. ilvensis* (B; Mount Obavskyi Kamin', Transcarpation region) (Vasheka & Bezsmertna 2012, modified). Scale bar = 1 cm.

Difficulties of *Woodsia* nomenclature

There are many errors in the distribution of the studied species in Ukraine due to their synonymous names. Difficulties can arise regarding the synonymy of the species, especially in the literary sources of the 19–20th century in comparison with modern nomenclature (Euro+Med 2006). Therefore, the emphasis here is not on the list of synonyms as such, but on the citations of names used in the Ukrainian literature. To clarify the misinterpretation of the distribution of the species in Ukraine, and in an effort to reduce the number of misunderstandings in the identification of the studied species in the literature, we present their extended taxonomic citations as follows:

***Woodsia alpina* (Bolton) S.F.Gray**, 1821, Nat. Arr. Brit. Pl., 2: 17; Fomin, 1926, Flora of USSR., 1: 24; Fomin, 1934, Flora of Ukrainian part of USSR, vol. 1: 23; Fomin, 1935, Flora of USSR, 1: 54; Fomin, 1938, Flora of USSR, 1: 47; Chater, 1964, Flora Europaea, vol. 1: 19; Bobrov, 1974, Flora of European part of USSR, vol. 1: 76; Chopyk, 1976, Alpine Flora of Ukrainian Carpathians: 17; Chopyk, 1977, Viznachnik roslin Ukrainskikh Karpat: 28; Prokudin, 1987, Opredelitel vysshikh rasteniy Ukrainy: 29; Didukh et al., 2000, Ekoflora Ukrainy, 1: 120. – ***Acrostichum alpinum* Bolton**, 1790, Fil. Brit.: 76. – ***A. hyperboreum* Liljebl.**, 1793, Kongl. Vet. Acad. Handl. 14: 201. – ***Woodsia hyperborea* R. Br.**, 1815, Trans. Linn. Soc. London (Bot.), 11: 173; Ledeb., 1853, Fl. Ross., 4: 511; Fedchenko & Flerov, 1910, Flora of European part of Russia, vol.1: 4. – ***W. pilosella* Rupr.**, 1845, Beitr. Pflanzenk. Russ. Reiches, 3: 54; Montrezor, 1898, Index of Plants collected in Kyiv Training District 33. – ***W. alpina* var. *bellii* G. Lawson**, 1864, Canad. Naturalist & Quart. J. Sci. 1: 4. – ***W. bellii* (Lawson) A.E. Porsild**, 1945, Rhodora 47(557): 147.

***Woodsia ilvensis* (L.) R. Br.**, 1810, Prodr. Fl. Nov. Holl., 1: 158; Ledeb., 1853, Fl. Ross., 4: 510; Shmalhauzen, 1886, Flora of South-Western part of Russia: 725; Fedchenko & Flerov, 1910, Flora of European part of Russia, vol. 1: 4; Fomin, 1926, Flora of Ukraine, vol. 1: 24; Wulf, 1927, Flora of Crimea, 1: 11; Fomin, 1934, Flora of Ukrainian part of USSR, vol. 1: 23; Fomin, 1935, Flora of Ukrainian part of USSR, 1: 53; Fomin, 1938, Flora of Ukrainian part of USSR, 1: 46; Chater, 1964, Flora Europaea, vol. 1: 19; Bobrov, 1974, Flora of European part of USSR, 1974, 1: 76; Chopyk, 1977, Viznachnik roslin Ukrainskikh Karpat: 28; Prokudin, 1987, Opredelitel vysshikh rasteniy Ukrainy: 29; Didukh et al., 2000, Ekoflora Ukrainy, 1: 122. – ***Acrostichum ilvense* L.**, 1753, Sp. Pl. 2: 1071. – ***Polypodium ilvense* (L.) Vill.**, 1789, Hist. Pl. Dauphiné, 3: 848. – ***P. arvonicum* Wither**, 1796, Bot. Arrang., 3: 774. – ***Nephrodium rufidulum* Michx.**, 1803, Fl. Bor. Amer., 2: 269-270. – ***Aspidium rufidulum* (Michx.) Sw.**, 1806, Syn. Fil. 58. – ***Notholaena setigera* Desv.**, 1813, J. Bot. Agric. 1: 93. – ***Athyrium rufidulum* (Michx.) A.A. Eaton**, 1817, Man. Bot. for N. S.: 122. – ***Notholaena rufidula* (Michx.) Desv.**, 1827, Mém. Soc. Linn. Paris, 6: 221. – ***Woodsia rufidula* (Michx.) L.C. Beck**, 1833, Bot. North. Mid. St.: 452. – ***Lastrea rufidula* (Michx.) C. Presl**, 1836, Tent. Pteridogr.: 76. – ***Woodsia intermedia* Rupr.**, 1845, Beitr. Pflanzenk. Russ. Reich. 3: 54. – ***W. raiana* Newman**, 1844, Hist. Brit. Ferns (ed. 2) 140. – ***W. hyperborea* var. *rufidula* (Michx.) W.D.J. Koch.**, 1845, Syn. Fl. Germ.

Helv. (ed. 2) 2-3: 975. – ***W. frigida* Gand.**, 1881, Oesterr. Bot. Z. 31(1): 18. – ***W. uralensis* Gand.**, 1881, Oesterr. Bot. Z. 31(1): 18; 2005, News of Taxonomy of Higher Plants 37: 7-32. – ***W. ilvensis* var. *rufidula* (Michx.) Asch. & P. Graebn.**, 1896, Syn. Mitteleur. Fl. 1: 45; Fedchenko & Flerov, 1910, Flora of European part of Russia, 1: 4. – ***W. ilvensis* var. *calcarea* Fomin**, 1930, Flora of Siberia and Far East 5: 21. – ***W. asiatica* Schmakov et Kiselev**, 1995, l. c.: 40.

***Woodsia* ×*gracilis* (Lawson) Butters**, 1941, Amer. Fern. Journ. 31, 1: 15; D. Brown, 1964, l.c.: 50, tab. 5a, 6; Smakov & Kiselev, 1995, cited: 28; Kucherov et al., 1988, In: Stud. of Biodivers. by Methods of Comp. Flor.: 120; Kulikov, 2004, Bot. J. 89, 3: 494. – ***W. ilvensis* var. *gracilis* Lawson**, 1864, Edinb. New Philos. Jour., N.S., 19: 281.

Distribution of the studied species in Ukraine

Correct records

Woodsia alpina is distributed in Central Europe, Scandinavia, Western and Eastern Siberia, Central Asia and North America (Meusel et al. 1965a, b; Jalas & Suominen 1972; Hultén & Fries 1986). It has been reported in the Carpathian region and the Steppe zone in Ukraine (Didukh et al. 2000; Didukh 2009; Peregrym & Didukh 2014), but the only correct records are from the territories of Steppe zone, where it has been confirmed from four localities.

The first locality is in the «Kam'yani Mohyly» department of the Ukrainian Steppe Nature Reserve (Kleopov 1925; specimen deposited in BP, DNZ, KW, KWHA, LWKS). This locality is mentioned in many published sources: Flora of the European part of the USSR (Fedorov 1974) and Flora of Ukraine (Fomin 1926; Prokudin 1987; Didukh et al. 2000; Didukh 2009; Ostapko et al. 2010).

The second locality is on Khortytsia Island on the Dnieper river (Zaporizhzhya region) (Popovych et al. 1992; Okhrimenko et al. 2016; Shelegheda & Shelegheda 2017). *Woodsia alpina* has also been found here by K. Ye. Koreshchuk (Khortytsia National Historical and Cultural Reserve) in the northern, rocky part of the island (Shelegheda & Rastvorova 2007; Shelegheda & Shelegheda 2017).

The third record is reported for the territory of Cherdakly Local Natural Monument (Donetsk region) (Mulenkova 2010) and a fourth locality is known in the vicinity of Miusyns'k (Luhansk region) (Peregrym & Didukh 2014; specimen deposited in KW).

Woodsia ilvensis occurs in Central Europe, Scandinavia, Western and Eastern Siberia, Central Asia, the Far East and North America (Meusel et al. 1965a, b; Jalas & Suominen 1972; Hultén & Fries 1986).

In Ukraine, isolated localities of the species are reported from the Ukrainian Carpathians, Ukrainian Polissia and Crimea. Its reported occurrence in the Steppe zone is erroneous and records from Crimea are questionable and remain unconfirmed (Pallas 1975; Wulf 1923; Popovych et al. 1992; Didukh et al. 2000; Didukh 2009).

The distribution of the species in Ukrainian Polissia is worthy of some discussion, as it now appears to be very restricted there. *Woodsia ilvensis* has been reported

from the territory of the Zhytomyr region by V. Montrezor, Yo. Pachoskyi, I. Shmalhauzen, M. Raciborski (Shmalhauzen 1886; Pachoskyi 1900; Montrezor 1886, 1889, 1898; specimen deposited in KRA, KRAM, KW, LE, WA); similar information is included in the Flora of Ukraine (Fomin 1926), Flora of the European part of the USSR (Fedorov 1974) and many other sources (Prokudin 1987; Didukh 2009). In total, six localities of the species were known in Zhytomyr region: within the limits of Zhytomyr city – on the rocks of Sokulia (current name – Holova Chatskoho Rock) and Chotyry Braty (Pachoskyi 1900; Fomin 1926, 1938; Kondratiuk 1950; specimen deposited in KRA, KRAM); in the vicinity of the former village Velyke Shumske (rocks above river Hnylopiat) (Fomin 1926, 1938; specimen deposited in KW, WA), as well as on Mount Osiianka (Burchak-Abramovych 1949; Melnyk 2000) in the vicinity of Sinhury village (rocks along Hnylopiat river, Skelia Krashevskoho Nature Monument) (specimen deposited in KWHU); in the territory of Korostyshiv district in the vicinity of Stryzhivka village on the bank of the Teteriv river (Pachoskyi 1900; Fomin 1926, 1938).

The populations of *W. ilvensis* that grew on granite walls on rocky banks of the Teteriv river have probably disappeared as a result of raising water levels by 17 m and flooding the lower parts of the rocks following the construction of a flax mill dam (Orlov et al., 2016). Mount Osiianka, which was located on the right bank of the Hnylopiat river (4 km to the South from the Teterivka village in Zhytomyr district), was completely destroyed as a result of granite quarrying and mining activity. A locality of the species in the vicinity of Stryzhivka village has not been confirmed, despite recent attempts, but it should be noted that currently there is no suitable granite habitat for the species in this area along the Teteriv river. Thus, the only extant location for this species in the Ukrainian Polissia is in the territory of the Skelia Krashevskoho geological natural monument on the right bank of the Hnylopiat river (Zhytomyr district) (Burchak-Abramovich 1949; Melnyk 2000; Orlov 2009; Orlov et al. 2016; specimen deposited in KWHU).

Regarding the distribution of the species in the Ukrainian Carpathians, *W. ilvensis* has been reported from several localities, in particular in the Transcarpathian region (Popov 1949). *Woodsia ilvensis* has been recorded from the Stinka Botanical Reserve (Velikoberezniansкyi district, Zakarpattia region; Uzhanskyi National Nature Park) in the Eastern Beskydy (Hadač 1996). This locality was noted from herbarium collections and a number of literature sources (Kricsfalusy & Lesyo 2004; Sabadosh 2010; specimen deposited in LWS); it has also been confirmed by us (Vasheka & Bezsmertna 2014; specimen deposited in KWHU).

There are literature reports of *W. ilvensis* growing in the foothills of the Carpathians in the territory of the Uzhhorod district of the Zakarpattia region (Chopyk 1977; Prokudin 1987; Chopyk & Fedoronchuk 2015). A sample of the species was collected by S. Fodor in 1960 in the vicinity of the village of Kamenytsia (Uzhhorod district), in the Skalka natural area in the foothills of the Carpathians (specimen deposited in UU). Unfortunately, our field research did not allow us to re-find or confirm its presence in this territory.

The species is also known from the Svydovets rock massif, in particular, Mount Kobyla (near the village of Kobyletska Poliana, Rakhiv district, Zakarpattia region) (Buček 1931; Fodor 1974; Chopyk 1976; Sabadosh 2010). A finding of *W. ilvensis* in the vicinity of Rakhiv, on the slopes of Svydovets, where the species grew on rocks in a beech forest was reported by Shushman (2008) and Sabadosh (2010). This record has also been confirmed by us (Hleb, Vasheniak & Bezsmertna 2018; specimen deposited in KWHU).

Additionally, *W. ilvensis* was found in the Volcanic ridge of the Carpathians, in particular, Mount Poprychnyi Verkh (Zakarpattia region, Perechynskyi district) (Chopyk 1977; Prokudin 1987; Kricsfalusy et al. 1999; Sabadosh 2010; Chopyk & Fedoronchuk 2015). Unfortunately, we did not find this locality and there are no herbarium specimens of the species from this place.

There are also references to *W. ilvensis* growing on the Marmaros rock massif in Zakarpattia (Margittai 1927): "*Eddig vidékünkön cask a Vihorlátról és a Szinna-Kőröl volt ismeretes. A nagyszőlősi Feketehegyen nem tudtam megtalálni e harasztot. Újabban Máramaros megyében a «Kamen» nevü hegy szikláin találtam meg Rahó mellett*". [Translation: "Until now, only Vyhorlat and Snina had it in our region. Unfortunately, I could not find this fern on Mountain Chorna near Vynohradiv city. Recently I have managed to find one of these plants in the Marmaros district on the rocky slopes of Mount Kamin near Rakhiv city."]. Herbarium specimens are also available from this area (Mount Kamin near Rakhiv city) in BRNU, BP, PRC. Based on the coordinates that are indicated on the herbarium sample, and in accordance with the toponyms in the vicinity of the city of Rakhiv, we consider this record to refer to Rachiw perewal (or Kamiń-Klewka). Unfortunately, our field research did not allow us to re-find or confirm its presence in this territory.

Doubtful (erroneous) or unconfirmed records

Woodsia alpina is erroneously mentioned for the territory of the Carpathian region. It is cited in a paper by Kricsfalusy & Lesyo (2004) as growing in the territory of the Eastern Beskydy, Stinka Botanical Reserve (Zakarpattia region, Uzhanskyi National Nature Park). However, this information has not been confirmed by herbarium collections. On the other hand, there are samples, literature data and our own records of *W. ilvensis* from this area.

Regarding the reported occurrence of *W. alpina* in the Chyvchyno-Hryniavsky Mountains (Chopyk 1976; Chopyk 1977; Prokudin 1987; Chopyk & Fedoronchuk 2015) only one herbarium specimen has been found for this territory (specimen deposited in KWHA). As a result of our research, an error was found in the identification of this specimen, and we re-identified it as *Dryopteris filix-mas* (L.) Schott. Below, we present information in accordance with the original label from the herbarium sheet: "Ivano-Frankivsk region, Kosiv district, Chyvchynsky mountains, under the top of Mountain Zanoga, between Bily`j and Chorny`j Cheremosh, upper border of the spruce forest. 30.07.1963. Collected and Identified by Chopyk V. I."

(Notae criticae: *Dryopteris*? Nadiya Sytschak, 02.12.2014; *Dryopteris filix-mas*, O. Bezsmertna, 10.10.2018).

Both species were also noted in the book "Montane element of the flora of the Ukrainian Carpathians" of A. Malynowskyi (1991), but only maps are given without precise species localities. It is assumed that this book indicates *W. alpina* as growing in the Carpathians erroneously. This assumption is drawn from the fact that we found a sample labelled *W. alpina* in the LWS herbarium: "Zakarpattia region, Rakhiv district, South-Eastern slope of Pietros. In the spruce forest near the road to Hoverla, on the rocks. 1550 m a.s.l. 22.08.1954. K. Malynowskyi". On re-examination, we determined this specimen to be *Asplenium viride* Huds. (Notae criticae: *Asplenium viride*, A. Zelenchuk, 1985; Vidi: O. Bezsmertna, 08.02.2011).

Additionally, a number of literature sources indicate that *W. alpina* is widespread in the Chornohirskyi mountain ridge (Fodor 1974; Prokudin 1987; Sabadosh 2010), in Gorgany Mountains (Chopyk 1976; Prokudin 1987; Sabadosh 2010) and in the Volcanic Carpathians (Chopyk 1976, 1977; Prokudin 1987; Kricsfalusy et al. 1999; Tsvelev 2005b; Sabadosh 2010).

As for the Volcanic Carpathians, in our opinion, the report of *W. alpina* probably refers to Mount Obavskyi Kamin'. This is supported by the fact that literature sources indicated this species or noted that it hybridizes with *W. ilvensis*.

Several literary sources list *W. alpina* for Mount Obavskyi Kamin' (Volcanic Carpathians) in the vicinity of Syniak village (Zakarpattia region) (Chopyk 1976, 1977; Chopyk & Fedoronchuk 2015). However, in 2014 on the top of Mount Obavskyi Kamin' in the vicinity of Syniak village, we found only one species – *W. ilvensis* (Bezsmertna & Votkalchuk 2014; specimen deposited in LW).

Regarding Chornohora ridge, we have not found reference to any locations of *W. alpina* in this region in the paper of Margittai (1937), referred to later by Fodor (1974).

Therefore, we believe that all these reported occurrences of *W. alpina* (Chorhohora, Chyvchynsky mountains, Horhany and Volcanic Carpathians) are erroneous, since there is currently no voucher specimen which would support the occurrence of the species there.

Woodsia alpina has also been erroneously mentioned for Ukrainian Polissia. The the distribution of both *Woodsia* species in this region has been the subject of much discussion. Some confusion arose on this issue at the end of the 19th century. V. Montrezor reported both species in various publications. In his first papers, V. Montrezor lists *W. alpina* under the synonymous name *W. hyperborea* (given without the author's instructions and variants or forms) (Montrezor 1889). In another publication, he indicates *W. ilvensis* (L.) R. Br. (mentioning its synonym *W. hyperborea* f. *rufidula*) (Montrezor 1886). In his next paper, "List of plants collected in the Kyiv educational district" (Montrezor 1898), he indicated both species for the Zhytomyr region. An interesting fact highlighted in the notes shows that *W. ilvensis* was firstly found in the territory of the Zhytomyr region in 1828, and confirmed by H. Sobkevych only in the 1880s; other locations became known at the time. This

information suggests and implies that both species occurred in the vicinity of Zhytomyr. However, attention should be paid to the notes in the same publication. In this connection, V. Montrezor cites *W. alpina* (*W. pilosella* Rupr. with the specified synonym *W. hyperborea* Lessing) and notes that this species grows beside *W. ilvensis*, found by H. Sobkevich and identified in the herbarium of the St. Petersburg Botanical Garden (Montrezor 1898). The specified herbarium specimen (or its duplicate) was found in the KW herbarium, but as a result of our research, was re-identified as belonging to *W. ilvensis* (Notae criticae: *Woodsia ilvensis*, Shmalhauzen; A. Fomin; Vidi: Alexander A. Kagalo, 30.10.2004; O. Bezsmertna, 07.04.2015). Thus, it is most likely that the vicinity of Zhytomyr has (and had) only one species growing – namely, *W. ilvensis*, which is also confirmed by the authors' revision of the mentioned localities (Orlov et al. 2016).

Woodsia ilvensis was mistakenly reported for Khortytsia Island on the Dnieper river (Zaporizhzhya region) (Steppe zone of Ukraine) (Popovych et al. 1992). Unfortunately, the herbarium specimen supporting this record has not been found (most likely missing). However, given the subsequent studies, where illustrative material is available and *W. alpina* is clearly identified (Okhrimenko et al. 2016; Shelegheda & Shelegheda 2017), we consider the report of *W. ilvensis* in this territory to be erroneous.

The occurrence of *W. ilvensis* in the territory of Crimea is questionable (Pallas 1975; Wulf 1923). Although the species was mentioned in the list of Crimean wild plants at the end of the 18th century, there are no exact locations given. Currently, there are no confirmed records in Crimea.

Thus, it can be concluded that for *W. alpina* in Ukraine, only four localities are known, and all are confined to the Steppe zone of Ukraine: two localities – in the Donetsk region, one in the Zaporizhzhya region and one in the Luhansk region. Interestingly, this montane species grows at an extremely low elevation. For example, the location of the Donetsk region stands at 106-182 m a.s.l., and the territory of the Lugansk region is 118 m a.s.l. and in Zaporizhzhia is only 30 m a.s.l. These locations are thought to be the lowest known in continental Europe (Kaplan et al., 2018; GBIF.org (14 December 2021)). The reported occurrence of *W. alpina* in the Carpathians and Ukrainian Polissia (Zhytomyr region) are considered to be erroneous (Fig. 4.).

For *W. ilvensis*, six localities are known in Ukrainian Polissia (Zhytomyr region), of which only one population has survived to this day. In the Carpathians, the following locations are confirmed from five localities in the Zakarpattia region: in the Eastern Beskydy (Uzhanskyi National Nature Park, Stinka Botanical Reserve), the foothills of the Carpathians (Skalka area, the vicinity of Kamianytsia village, Uzhhorod district), on the Svydovets rock massif (Mount Kobyla, slopes of the Kobyletska Poliana, Rakhiv district), on the Maramoros mountains (Kamiń-Klewka, Rakhiv district), and in the Volcanic Carpathians (Mount Obavskyi Kamin', near Synyak village, Mukachevo district). Species occurrence in the Volcanic Carpathians (Mountain Poprychnyi

Verkh) requires confirmation. Reports of the species in the Autonomous Republic of Crimea and the Zaporizhzhya region are incorrect (Fig. 5).

Hypothesis about the occurrence of montane *Woodsia* species in the plain territories of Ukraine

Several scientists of different periods have focussed their attention to the study of the occurrence of montane species on the lowland plains of Ukraine and adjacent territories. There are many examples of the occurrence of montane species on the plain territories: *Cardamine glanduligera* O. Schwarz, *Erythronium dens-canis* L., *Symphytum cordatum* Willd., *Carex depressa* subsp. *transsilvanica* (Schur) T. V. Egorova (Rehman 1886; Paczoski 1910; Szafer 1923, 1930; Zaverukha 1985; Malynowskyi 1991).

In the case of *W. ilvensis*, and its occurence in Ukrainian Polissia, it is probably a mutual refugium with *Asplenium septentrionale* (L.) Hoffm. and a member of the pre-glacial relict flora which has remained on the diluvial surface sediments formed as a result of glacial dam burst at the end of the last ice age (Szafer 1923).

Regarding *W. alpina* and its occurrence on the plain, and bearing in mind that *W. alpina* is a tetraploid of *W. glabella* Richardson and *W. ilvensis* (Cody & Britton 1989; Larsson 2014), both circumboreal species (Meusel 1965a, b), it is suggested that in the process of evolution their locations on the plain are refugia of the postglacial period. This theory is supported by the disjunctive distribution of their current populations today. Just as *W. ilvensis* might have migrated to the territory of Ukraine from the western part of Europe, judging from the large number of records there (GBIF.org (30 January 2022)), *W. alpina* could be a remnant of the Caucasian flora that spread via the Caucasian pathway through the Kerch-Tamanian bridge (Iena 2012). The current populations in the Caucasus Mountains are the closest in proximity to those found in the southern Ukrainian steppe zone, but much more detailed genetic research is required on populations in Ukraine, the Carpathian and Caucasian regions and in Europe generally, in order to answer questions on the origins of the Ukrainian plants.

Another consideration that may help to explain the occurrence of *W. alpina* in the lowland plain is the local geology. Much of the lowland plain consists of outcrops of granite rocks of the Ukrainian Crystal Shield (Bondarchuk 1959). These rocks can create favourable microclimatic conditions, similar to those in alpine areas, with high humidity levels in crevices providing a microclimatic refugia for relict species such as *W. alpina* (Ellenberg 1974; Ellenberg et al.1991; García et al. 2020; Ranđelović et al. 2021). Although relatively few such refugia were examined during the present study, with the benefit of this new understanding of the importance of such niches for *W. alpina*, it is possible that new localities may be discovered in southern Ukraine. It is also worth noting that searching for such habitats in Crimea may yield further populations.

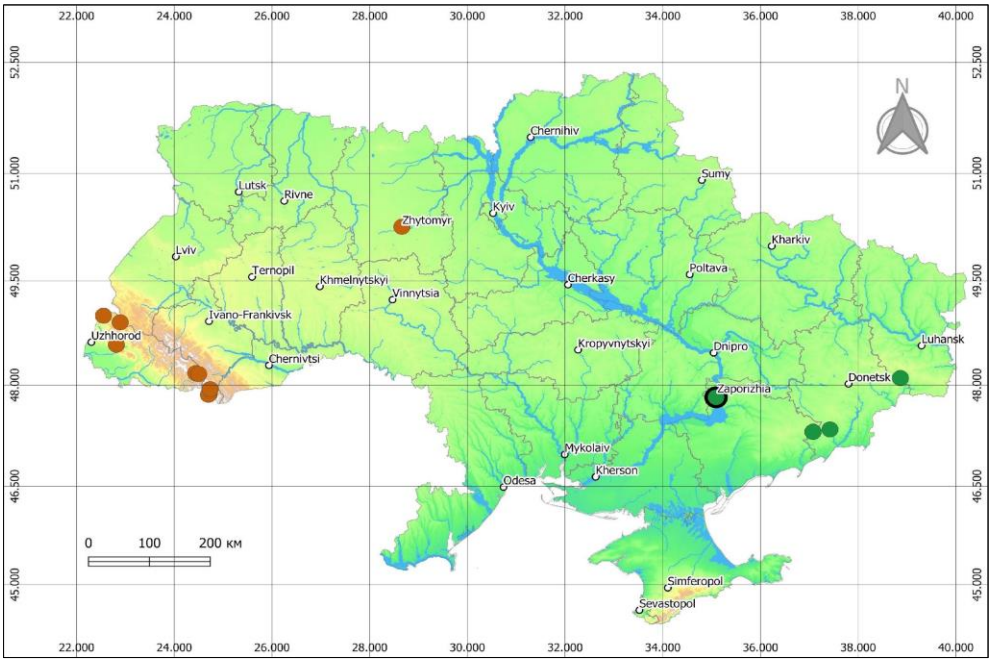

Fig. 4 Distribution of *Woodsia alpina* in Ukraine according to our revision. Dark green colour indicates confirmed locations and red colour indicates locations that are erroneous. Outlined circle indicates that this locality consisted of two species records before our revision but only one species has been confirmed to occur.

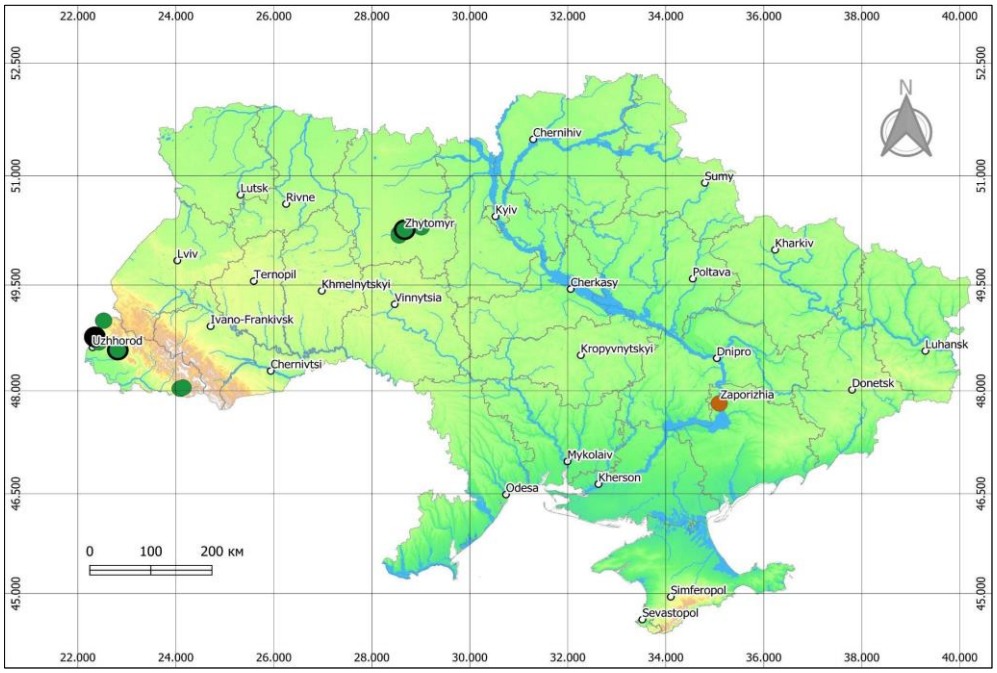

Fig. 5 Distribution of *Woodsia ilvensis* in Ukraine according to our revision. Dark green colour indicates valid locations, black colour indicates the locations that need confirmation and red colour indicates locations that are erroneous. Outlined circles indicate that this location consisted of two species records before our revision but one species has been confirmed to occur.

Populations

Both studied species grow on acidic rock outcrops (siliceous rocks, granites, andesites) and only very rarely on outcrops of conglomerates. In general, all populations of both species are currently small (do not exceed 20 clonal individuals) and occupy small areas. Most often, the average area occupied by populations is about 0.5 m^2. The maximum area occupied by populations is 10 m^2 in the Zhytomyr region and 5 m^2 in Zakarpattia.

Populations of *W. alpina* have a maximum of ten individuals in the vicinity of Miusyns'k (Luhansk region) and in the territory of the Kam'yani Mohyly Nature Reserve (Donetsk region) in several locations (Lyalyuk et al. 2012; Peregrym & Didukh 2014). For instance, in the territory of the Kam'yani Mohyly Nature Reserve, *W. alpina* grows in three localities (Lyalyuk et al. 2012) and is represented in total by eight individuals (five, two and one, respectively). The population in the Cherdakly Botanical Reserve of Local Significance is described as small but with stable renewal (Mulenkova 2010). There is no information on the population on the island of Khortytsia (Popovych et al. 1992; Shelegheda & Rastvorova 2007; Okhrimenko et al. 2016; Shelegheda & Shelegheda 2017).

Confirmed populations of *W. ilvensis* are also scanty and occupy small areas. In particular, only two individuals were found on Mount Kobyla in an area of about 0.5 m^2, and six plants (5 m^2) were found in the Stinka Botanical Reserve in the territory of the Uzhanskyi National Nature Park. The largest number of plants, covering a larger area (up to 5 m^2), was observed in the populations in the Zhytomyr region and on Mount Obavskyi Kamin' (Carpathians). In particular, the locality in the Skelia Krashevskoho Geological Nature Monument (Zhytomyr district) comprised about 100 individuals in 1990 (verbal communication of Doctor of Biological Sciences, Prof. T. L. Andrienko), but has now decreased to 20 individuals, mainly due to recreational pressure (trampling, burning, hiking), although young plants are still evident. It should be noted that the state of the species' population in the Skalka area, located in the foothills of the Carpathians and on the Mountain Poprichnyi Verkh (Volcanic Carpathians), is now unknown.

To summarise the discussion of distribution of the species in Ukraine, as well as to characterise the populations identified during our expeditions, below is a table of the confirmed localities. Sources of information are indicated, from the literature, from herbarium specimens, and whether we have found these populations during our investigations (Tab. 1) (Bezsmertna et al. 2021).

Phytosociological and ecological features of *Woodsia* populations

Observed plant communities with *W. ilvensis* are confined not so much to a certain rock types, but rather to relatively dry, well-lit, steep, open rocky slopes (steepness of 70 degrees or even more) on the border between exposed rock and forest vegetation, and fairly nitrogen-rich soils. This concurs with published data (Kolbek 1978; Mucina 1993; Valachovič 1995; Wendelberger 1967). *Woodsia alpina* can

Tab. 1 Confirmed locations of *Woodsia* species in Ukraine.

№	Locality	Literature	Herbarium	Own finding	Size of population (m^2)	Number of individuals (rosettes)
Woodsia alpina						
1	Donetsk region, Kam'yani Mohyly	+	+	+	less than 1	5, 2 and 1
2	Donetsk region, Cherdakly	+	-	-	unknown	unknown
3	Lugansk region, Miusyns'k town	+	+	-	0,5	10
4	Zaporizhzhya region, Khortytsia Island	+	-	-	unknown	unknown
Woodsia ilvensis						
1	Zhytomyr region, Skelia Krashevskoho Geological Nature Monument	+	+	+	10	Reduced from 100 to 20 (in present time)
2	Zakarpattia region, Stinka Botanical Reserve	+	+	+	5	6
3	Zakarpattia region, Skalka area	+	+	-	unknown	unknown
4	Zakarpattia region, Mount Obavskyi Kamin'	as *W. alpina*	-	+	5	20
5	Zakarpattia region, Mount Kobyla	+	-	+	0,5	2
6	Zakarpattia region, Mount Poprychnyi Verkh	+	-	-	unknown	unknown
7	Zakarpattia region, Kamiń-Klewka	+	+	-	unknown	unknown

often be found in niches with higher humidity than the surrounding dry, well-lit rocky slopes, e. g. rock crevices.

Communities with *W. alpina* in the vicinity of Miusyns'k (according to the Peregrym & Didukh 2014) occur on steep silicate rocks, where the moss-lichen layer is formed by diagnostic species of the alliance *Hypno-Polypodion vulgare* Mucina in Grabherr et Mucina 1993: *Hypnum cupressiforme* Hedw., *Polytrichum commune* Hedw., *Brachythecium rutabulum* (Hedw.) Schimp. Among vascular plants, there are ferns – *Polypodium vulgare* L., *Asplenium septentrionale* and *A. trichomanes* L. In general, such cenoses are typical for sites with both *W. alpina* and *W. ilvensis*, and they mainly formed by mosses and ferns.

In the territory of Kam'yani Mohyly, *W. alpina* grows together with *Asplenium ruta-muraria* L., *Dianthus carthusianorum* L. and *Festuca* sp. Such cenoses grow on granite rocks (in the rock crevices) and are characterised by poor grass cover, not exceeding 30 %. Lichens are represented by species of genus *Lepraria* Ach. Mosses are represented by *Grimmia laevigata* (Brid.) Brid., *G. longirostris* Hook., *G. pulvinata* (Hedw.) Sm., *Orthotrichum* sp., *Hedwigia ciliata* (Hedw.) P. Beauv (Boiko 2017).

In the territory of Zhytomyr region, *W. ilvensis* (at the top and on the vertical wall with 70° or more inclination, 200 m a.s.l.) grows on quartz-limestone rocks. The total cover of this cenoses was 60 %, consisting mainly of mosses and lichens. Mosses are represented by *Grimmia laevigata*, *G. longirostris*, *G. muehlenbeckii* Schimp, *G. pulvinata*, *Orthotrichum anomalum* Hedw., *Schistidium apocarpum* (Hedw.) Bruch & Schimp., *Hedwigia ciliata*, *Homalothecium sericeum* (Hedw.) Schimp., *Hypnum cupressiforme* Hedw. (Virchenko & Orlov 2009). Lichens are represented by species

of genuses *Lepraria*, *Physcia* (Schreb.) Michx., *Candelariella* Müll.Arg. and species *Xanthoparmelia stenophylla* (Ach.) Ahti & D. Hawksw., *Parmelia sulcata* Taylor, *Lepraria* cf. *membranacea* (Dicks.) Vain., *Acarospora fuscata* (Ach.) Arnold. Ferns are represented by *Asplenium septentrionale* and *A. ruta-muraria* L. Flowering plants include *Chamaecytisus* sp. Link, *Hypericum perforatum* L., *Festuca* sp. and *Solidago virgaurea* L.

Communities with *W. ilvensis* in Zakarpattia (Svydovetskyi rock massif, at the summit of Mount Kobyla, 1077 m a.s.l.) grow on quartz-limestone rocks on rendzic leptosols, as well as on micro-profile, gravelly soils, rich in humus, with an average thickness of 5 cm. The total cover of this cenoses was 80 %, consisting mainly of mosses and lichens. Succulents dominate in the E_1 layer (*Sedum hispanicum* L., *S. alpestre* Vill., *Hylotelephium maximum* (L.) Holub., *Saxifraga paniculata* Mitt.), with grasses (*Festuca saxatilis* Schur, *Poa compressa* L., *P. nemoralis* L., etc.). The moss-lichen layer is represented by the following species: *Polytrichum formosum* Hedw., *P. piliferum* Hedw., *Dicranum scoparium* Hedw., *Hypnum cupressiforme*, *H. jutlandicum* Holmen & Warncke, *Plagiothecium undulatum* (Hedw.) Schimp. Lichens include *Cladonia pyxidata* (L.) Hoffm. and *C. foliacea* (Huds.) Willd. In the E_1 layer, *Genista tinctoria* L., *Vaccinium myrtillus* L. and *Origanum vulgare* L. indicate that such cenoses are undergoing successional changes and are gradually overgrowing with forest species. *Sempervivum marmoreum* Griseb, a very rare species in the flora of Ukraine, is also found at this location (Kobiv et al. 2007).

Other communities with *W. ilvensis* in Zakarpattia (Uzhanskyi National Nature Park, Stinka Botanical Reserve, at the top and 80° inclination, 1092 m a.s.l.) grow on sandstones in the ridge part of the mountain range. The total cover of this communities is about 80 %, including mosses, ferns and lichens. Mosses are represented by the following species: *Bryoerythrophyllum recurvirostrum* (Hedw.) P.C.Chen, *Grimmia hartmanii* Schimp. *G. pulvinata*, *Orthotrichum anomalum* Hedw., *Schistidium apocarpum* (Hedw.) Bruch & Schimp., *Bryum argenteum* Hedw., *Ptychostomum imbricatulum* (Müll. Hal.) Holyoak & N. Pedersen. Ferns are represented by *Polypodium vulgare*, *Asplenium septentrionale*, *A. trichomanes* and *A. ruta-muraria*. *Dianthus carthusianorum* and *Hylotelephium telephium* (L.) H. Ohba. are also present.

Another community with *W. ilvensis* in Zakarpattia (Zakarpattia region, Mount Obavskyi Kamin', at the top and on the vertical wall, 970 m a.s.l.) also grows on sandstone ridges. The total cover of these communities is about 30 %, including mosses, ferns and lichens. Lichens are represented by species of genus *Xanthoparmelia* (Vain.) Hale, *Cladonia* P. Browne, *Lecanora* Ach. and *Lepraria*. Mosses are represented by *Grimmia* sp., *Schistidium apocarpum*, *Orthotrichum* sp., *Bryum argenteum* and *Hedwigia ciliata*. Ferns are represented by *Asplenium septentrionale*. Other vascular plants are represented by the following species: *Calamagrostis arundinacea* (L.) Roth., *Festuca* sp., *Hieracium* sp. L. and *Solidago virgaurea* L.

Analysing the floristic composition of such communities and comparing them with the descriptions of the alliances *Asplenio-Festucion pallentis* Zólyomi 1936 corr. 1966 and *Diantho lumnitzeri-Seslerion* (Soó 1971) Chytrý et Mucina in Mucina et Kolbek 1993, we found that there are clear differences between relevés made in Ukraine and those from Central Europe (Sádlo & Chytrý 2009). The presence of species diagnostic of the class *Elyno-Seslerietea* Br.-Bl. 1948 (*Sedum alpestre*, *Thymus alpestris* Tausch) are evident. However, the floristic core of such vegetation is not represented in Ukrainian communities, so it is impossible to state whether these communities belong to this class. Nevertheless, a number of diagnostic species of the class *Asplenietea trichomanes* (Br.-Bl. In Meier et Br.-Bl. 1934) Oberd. 1977, the alliance *Asplenion septentrionalis* Gams ex Oberd. 1938 are represented: *Polypodium vulgare*, *Asplenium septentrionale*, *Poa nemoralis*, *Cladonia pyxidata*, *Polytrichum piliferum* and *Dicranum scoparium*.

The floral core of the alliance *Asplenion septentrionalis* is ambiguously distinguished, and there are also species that may indicate a generic relationship of communities with *Elyno-Seslerietea* or *Trifolio-Geranietea*.

According to the literature sources (Sádlo & Chytrý 2009; Peregrym & Didukh 2014), we provide a provisional and preliminary syntaxonomical scheme to the alliance level. However, we are planning to continue our work to take into account the phytosociological and ecological peculiarities of *W. ilvensis* and *W. alpina* in the Carpathian region, using the EVA database (Chytrý et al. 2016) and our data from Ukraine:

Cl. *Asplenietea trichomanes* (Br.-Bl. in Meier et Br-Bl. 1934) Oberd. 1977
  Ord. *Asplenietalia septentrionalo-cuneifolii* Mucina et Theurillat 2015
    All. *Asplenion septentrionalis* Gams ex Oberd. 1938
Cl. *Polypodietea* Jurko et Peciar ex Boşcaiu, Gergely et Codoreanu in Raţiu et al. 1966
  Ord. *Hypno cupressiformi-Polypodietalia vulgaris* Jurko et Peciar ex Mucina et Theurillat 2015
    All. *Hypno-Polypodion vulgare* Mucina 1993

The studied species of *Woodsia* are characterised by a pioneering strategy, which is manifested in their extremely weak competitiveness. Judging from their restricted occurrence to particular substrates, *Woodsia* species in Ukraine are typically petrophytic, with a preference for acidic rocks (Zarzycki et al. 2002; Zarzycki 2008). The optimum condition for *Woodsia* populations was observed exclusively at the pioneer stage of rock vegetation development. There is a gradual suppression of *Woodsia* populations in transitional to post-pioneer stages of primary successions, and a complete loss of the species in post-pioneer vegetation.

Pioneer and post-pioneer stages of rock overgrowth in *Woodsia* habitats, in the absence of developed cover of vascular plants, can be diagnosed by moss cover. In the post-pioneer stages, the substrate confinement of moss communities can be determined by the parameters of initial soils, particularly by soil humidity.

Ecological ranges:

1 – Pioneer stage

A* – Siliceous rocks (Kam'yani Mohyly, Skelia Krashevskogo, Obavskyi Kamin'): epilithic bryophytes community on siliceous substrates Cl. *Grimmio-Racomitrietea heterostichi* (Neumayr 1971) Hertel 1974, All. *Grimmion commutatae* v. Krusenstjerna 1945 (*Grimmia laevigata*, *G. longirostris*, *Hedwigia ciliata*, *Ceratodon purpureus* (Hedw.) Brid., *Bryum argenteum*, *Ptychostomum imbricatulum*).

2 – Post-pioneer stage

B* – Shaded rocks with sandy substrates (Kobyla, Obavskyi Kamin'): humicolous, mesophilous, sciophilous): Cl. *Hypnetea cupressiformis* Jezek & Vondracek 1962, All. *Dicrano scoparii-Hypnion filiformis* Barkman 1958 (*Polytrichum formosum*, *Dicranum scoparium*, *Hypnum cupressiforme*, *H. jutlandicum*, *Plagiothecium undulatum*).

C* – Shaded rocks with argilous and loamy substrates (Skalka): humicolous, mesophilous, sciophilous: Cl. *Pogonato-Dicranelletea heteromallae* v. Hubschmann 1967, All. *Brachythecienion velutini* Marstaller 1984 (*Plagiochila porelloides* (Torr. ex Nees) Lindenb., *Fissidens taxifolius* Hedw, *Plagiothecium cavifolium* (Brid.) Iwats., *P. nemorale* (Mitt.) Jaeg, *Brachytheciastrum velutinum* (Hedw.) Ignatov & Huttunen).

*Depending on the direction of primary soil formation, different combinations of options A and B / C are possible.

Conservation, species threat status and recommendation

The current threat status of *W. aplina* and *W. ilvensis* in Ukraine is "Endangered" (Didukh 2009). However, due to the low number of locations, small population size and threats facing both species in Ukraine, we recommend a re-assessment of the status of *W. alpina* and *W. ilvensis* to Critically Endangered (CR) (B2ab(ii,iii); C2a(i)) according to IUCN Red List Categories and Criteria (IUCN 2012).

Moreover, in the neighbouring countries studied, both species are also considered threatened and are included in regional red lists. For example, *W. alpina* and *W. ilvensis* are both threatened in Poland (red list status CR) (Kaźmierczakowa et al. 2016) and Slovak Republic (red list status VU) (Turis et al. 2014; Eliáš et al. 2015). In both the Czech Republic and in Hungary, *W. ilvensis* is listed as EN and *W. alpina* is considerd regionally extinct RE (Grulich & Chobot 2017; Király 2007). In Romania, following its recent discovery in the southern Carpathians, *W. alpina* has been reassessed from EN to critically endangered CR (B2ab(ii,iii,iv); C2a(i); D1) (Dihoru & Negrean 2009; Ranđelović et al., 2021; Sabovljević et al. 2021).

Given that both species are threatened in Ukraine and in several of the neighbouring European countries, we can assume that they are environmentally demanding and that their conservation depends on many factors. Although both species are regarded as Least Concern in Europe as a whole (Christenhusz et al. 2017a, b), with their main centres of distribution being found in Scandinavia and the Alps (GBIF.org (14 December 2021)), the populations in Ukraine and neighbouring countries are very small and fragile, especially for *W. alpina* (Dihoru & Negrean 2009; Kaplan et al. 2018; Zięba et al. 2020). Such outlying populations are clearly in decline

and are particularly important for conservation. For this reason, it is important to continue to investigate and monitor population trends and to understand the reasons for their decline.

Conclusion

To conclude, in the territory of Ukraine *Woodsia alpina* is distributed only in the territory of Donetsk, Luhansk and Zaporizhzhya regions (Steppe zone of Ukraine), and *W. ilvensis* only in the Zhytomyr region (Ukrainian Polissia) and Zakarpattia region (Ukrainian Carpathians).

The populations of both species are small: they consist of no more than ten individuals each and usually cover an area less than 0.5 m^2, and only a few populations cover an area up to 5 m^2. They are confined not so much to a certain type of rock, but to dry, well-lit steep, open rocky slopes (70° or more inclination) with thin, stony, nitrogen-rich soils at the border of rock and forest vegetation.

Despite the small area and the small number of individuals in the populations, the environmental conditions appear to be relatively stable over time (excluding anthropogenic influence). However, these populations are still vulnerable and at risk of local extinctions, due mostly to invasion by shrub vegetation. This can cause both reductions in light levels, through increased shading, and complete loss of suitable open, rocky habitat. This has been confirmed by the fact that *Woodsia* populations have survived in locations with significant recreation pressure (Kamiani Skeli, Skelia Krashevskogo, Obaskyi Kamin'). We believe the main reason for the disappearance of *Woodsia* populations is the process of spontaneous overgrowing with forest species (Carpathian region) that causes further petrophilous succession. In the post-pioneer stages (Kobyla, Stinka) *Woodsia* populations are stressed and on the Skalka Mountain they are absent.

Thus, the most important factor for the survival of *Woodsia* populations is the availability of suitable habitat niches. Such niches can be found where petrophilous vegetation sucession is held at a pioneer stage. This can occur on suitable rock outcrops in the steppe zone where the dry climate prevents the growth of woody vegetation. Similar niches can also be found in mixed-forest (Skelia Krashevskogo) or mountain-forest (Obavskyi Kamin'), where tree growth does not overtop large boulders and edaphic factors prevent vegetation succession.

Where the development of forest vegetation is not limited by climatic and edaphic factors, there is usually a gradual loss of *Woodsia* species. However, in the mountain-forest zones, where pioneer habitats are constantly forming due to weathering of the rocks, the populations of *Woodsia* mostly have a transitory character. Thus, in future it will be necessary to look for suitable *Woodsia* habitat niches in the areas of fresh outcrops.

In order to conserve these rare species in Ukraine, it will be necessary to monitor their populations regularly and to undertake management measures to maintain their open habitat where necessary. Taking into consideration the significantly changed perceptions of *Woodsia* distribution in Ukraine (i.e., according to our results

W. alpina is absent in the Ukrainian Carpathian region), it is advisable to review the distribution and status of *W. alpina* in the Carpathian region of adjacent territories. According to our research results, we recommend that the threat status for both species within Ukraine should be revised and re-evaluated to Critally Endangered. We recommend carrying out molecular genetic research on the Caucasus and Ukrainian *W. alpina* plants to answer questions about the origin of the southern Ukrainian populations. There is also a need for detailed research on population trends in the whole Europe, particularly on those populations on the periphery of the large centers of distribution, such as in Scandinavia and in the Alps.

Acknowledgement

We are warmly grateful to Olexandr Khodosovtsev (Kherson State University, Ukraine) for the helping with the lichen determinations. We express our sincere gratitude to Tibor Lubka (Transcarpathian Hungarian Ferenc Rakoczi II Institute, Ukraine) for the translation from the Hungarian language. We are most grateful to Timur Himranov (The Society for Conservation GIS) for assistance in processing of geodata. Many thanks to the curators of herbarium collections from different countries, who responded and provided the necessary information. This was very important to improve our article in the context of limited pandemic mobility, particularly to Marcin Nobis (Jagiellonian University, Poland), Maja Graniszewska (University of Warsaw, Poland), Hermann Voglmayr (Universität Wien, Austria), Jiří Danihelka (Masaryk University, Czech Republic), Beata Paszko (W. Szafer Institute of Botany, Polish Academy of Sciences, Poland), Marcin Zych (University of Warsaw Botanic Garden, Poland), Júlia Tamás and Beáta Papp (Hungarian Natural History Museum, Hungary), Patrik Mráz and Michal Štefánek (Charles University, Czech Republic), Tanja M. Schuster (Naturhistorisches Museum Wien, Austria), Krzysztof Świerkosz and Ewa Lenard (Wroclaw University, Poland), Adrian Oprea (Alexandru Ioan Cuza University, Romania), Lenka Mártonfiová (P. J. Šafárik University in Košice, Slovak Republic), Kurt Zernig (Universalmuseum Joanneum, Austria), Eliška Gbúrová Štubňová (Slovak National Museum, Slovak Republic), Hrabovský Michal (Comenius University, Slovak Republic), Tatiana Miháliková (Slovak Academy of Sciences, Slovak Republic), Mihai Puşcaş (Babes-Bolyai University, Romania). We are grateful to Handling Editor Matej Dudáš and two anonymous reviewers for valuable suggestions and comments that significantly helped to improve the manuscript. We are also grateful to Neil Lockhart (Bryologist, National Parks and Wildlife Service, Government of Ireland) for proofreading our manuscript.

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Received: September 10th 2021
Revised: October 21st 2021
Accepted: February 7th 2022